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Feeding and damage-induced volatile cues make beetles disperse and produce a more even distribution of damage for sagebrush

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ABSTRACT

1. Induced plant responses to herbivory are common and we have learned a lot about the mechanisms of induced resistance and their effects on herbivore performance. We know less about their effects on herbivore behavior and especially on spatial patterns of damage.

2. Theoretical models predict that induced responses can cause patterns of damage to become aggregated, random, or even. A recent model predicted that informed herbivore movement coupled with communication between plants would make damage more even within individual plants. We tested these predictions in the field using a specialist beetle (*Trirhabda pilosa*) that feeds on sagebrush (*Artemisia tridentata*). Both the beetle and the plant are well-documented to respond to damage-induced volatile cues.

3. Beetle larvae were more likely to move from damaged leaves and leaves that had been exposed to volatiles from nearby damaged leaves compared to undamaged control leaves. Previous lab results indicated that beetles were more likely to choose undamaged leaves compared to damaged leaves or those exposed to volatile cues of damage.

4. A comparison of damage patterns early in the season and after completion of beetle feeding revealed that variance in damage among branches decreased as the season progressed; i.e., damage became more evenly distributed among the branches within a plant. Larvae

damaged many leaves on a plant but removed relatively little tissue from each leaf.

5. Herbivore movement and the spatial patterns of damage that it creates can be important in determining effects on plant fitness and other population processes. Dispersion of damage deserves more consideration in plant-herbivore studies.

Key-words: induced resistance, spatial distribution, over-dispersed, herbivore behavior, movement, plant communication, dispersion, *Trirhabda*

1 INTRODUCTION

Anyone who has collected tree leaves at the end of the growing season knows that finding a leaf with no damage is rare. This pattern is counter-intuitive since many chewing insects (and other animals) are patchily aggregated in nature. This paper will consider one ecological process that could produce the scarcity of completely undamaged leaves.

Scientists have been aware of induced plant responses to herbivory for approximately 50 years (Green and Ryan 1972). When plants are damaged by feeding herbivores, they change in many ways and some of these changes make them less preferred and/or less suitable for herbivores. Induced responses propagate over various temporal and spatial scales, although many have been observed to be localized to those tissues that surround the site of damage (Karban and Baldwin 1997). Several of the early ecologists who described induced responses characterized these temporal and spatial changes and their effects on herbivores. For example, experimentally damaged squash leaves produced chemicals that spread from the site of wounding and rapidly changed the attractiveness and palatability of those damaged leaves for beetle larvae (Carroll and Hoffman 1980). Beetles were presumed to have moved away from sites that had been previously attacked since larvae and adults were always found at least 2 m from past feeding scars and beetles were never observed to occupy the

same leaf as a conspecific. Edwards and Wratten (1983) examined herbivore damage to leaves of clover and eight forest tree species at the end of the growing season. Although no statistical analyses were performed, they proposed that the pattern of damage was highly dispersed, i.e., all leaves had some relatively low level of feeding damage and few leaves had high levels. These authors speculated that plant responses and subsequent insect behavior could limit the total amount of tissue damage and that damage that was spread evenly among branches within an individual would be less detrimental to the plant than clumped damage.

In the decades since researchers first documented induced responses there has been considerable effort to elucidate the mechanisms that were responsible for plant perception and plant reactions to herbivores. Far less emphasis has been placed on understanding the spatial extent of induction and its consequences. Edwards and Wratten (1983) observed that insects tended to move away from damaged leaves and that this pattern of movement could produce an even pattern of damage at the scale of individual plants. Many herbivorous insects have been found to move away from previously damaged tissues (e.g., Edwards and Wratten 1983, Bergelson, Fowler, & Hartley 1986, Harrison and Karban 1986, Roslin et al. 2008, Kallenbach, Bonaventure, Gilardoni, Wissgott, & Baldwin 2012, Perkins et al. 2013, Morrell and Kessler 2017). Although this

pattern is commonly found, exceptions have also been noted even for insect species that feed on the same plants reported in the studies above (e.g., Carroll and Hoffman 1980, Bergelson and Lawton 1988).

Herbivores that avoid plant tissues that have been damaged previously are considered to exhibit 'informed herbivore movement' (sensu Rubin, Ellner, Kessler, & Morrell 2015). There has been little consensus concerning whether informed herbivore movement will produce even damage to host plants. For example, models of herbivore movement away from damaged-induced plant tissue often predict that herbivores will aggregate at tissues of higher quality (Underwood, Anderson, & Inouye 2005, Anderson, Inouye, & Underwood 2015). This was the pattern observed for beetles on damaged soybean foliage (Underwood, Anderson, & Inouye 2005). A more complex model that included informed herbivore movement as well as volatile communication between neighboring plants was parameterized with empirical data from *Trirhabda virgata* beetles feeding on goldenrod; this model generated distributions that ranged from even to aggregated (Rubin, Ellner, Kessler, & Morrell 2015). These authors found that induced plant resistance tended to lead to patterns of aggregated damage but the addition of both informed herbivore movement and communication between plants spread the damage more evenly.

Although there is considerable empirical evidence that many herbivores preferentially move away from damage (informed movement), the effects of this movement on the distribution of damage is poorly understood. It is not known how movement affects the distribution of damage for plant species that respond to cues emitted by damaged neighbors although many plants have been found to exhibit these responses (Karban, Yang, & Edwards 2014). Sagebrush (*Artemisia tridentata*) induces resistance when directly attacked by herbivores or when exposed to damage-associated VOCs produced by experimentally wounded tissue of neighbors (Karban, Shiojiri, Huntzinger, & McCall 2006). In this case, induced resistance was assayed by measuring reductions in the total herbivore damage accumulated over the growing season. Behavioral assays have also been conducted in petri dishes in the lab involving locally abundant chrysomelid beetle larvae (*Trirhabda pilosa*) presented with induced or uninduced sagebrush leaves (Grof-Tisza, Karban, Pan, & Blande 2020). These bioassays indicated that beetles consistently chose undamaged control leaves in preference to leaves that had been either damaged or exposed to volatiles from damaged leaves. In this current study we asked whether beetle larvae in the field were more likely to move to another leaf if the leaf they were on was experimentally clipped or exposed to volatiles from a nearby damaged leaf compared to controls. We then asked whether this movement reduced the variation

in damage among branches within sagebrush plants. We flagged all of the branches on study plants and recorded whether the distribution of damage changed from the beginning to the end of the time when these univoltine beetles fed on sagebrush.

2 Methods

2.1 Study System

Sagebrush is the most abundant and the defining plant of the Great Basin biome of western North America (Young, Evans, & Major 1988). This study was conducted at the UC Valentine Eastern Sierra Reserve (N 37.631 W -118.996) at an elevation of 2550 m, near Mammoth Lakes, CA. Several subspecies of sagebrush co-occur at this study site although only the subspecies *vaseyana* was considered in this study. As a result of its abundance and widespread distribution, sagebrush serves as the host for a large list of insect and vertebrate herbivores (Wiens et al. 1991, Sanford and Huntley 2010).

Bushes at the study site were attacked by a specialist chrysomelid beetle (*Trirhabda pilosa*) during the summers of 2017 – 2019. This outbreak may have occurred in previous summers but escaped our notice. Populations of this beetle are very patchy such that some bushes had 100% of their leaves attacked while those less than 1 km away supported no larvae. Eggs overwinter in the soil or under bark and larvae begin feeding on foliage at the elevation of this study in late June or early July (Pringle 1960). Feeding by larvae of *T.*

pilosa is recognizable as rasping damage that leaves a hole or skeletonized pattern with uneven margins in the interior of leaves. This unusual characteristic of damage can be readily differentiated from that caused by the other herbivores of sagebrush in eastern California. Larvae have not been observed feeding on any other host species (Pringle 1960, Karban pers. obs.) Beetles pupate in the soil beneath bushes by mid July. Adults feed on inflorescences and foliage of sagebrush and mate in late July and August.

Movement

We tested whether larvae were more likely to move if the leaf on which they were located was experimentally clipped. We recorded whether 100 individual beetle larvae remained for one hour on the leaves where they were first observed. The leaf or nearby stem was marked with a small piece of colored lab tape. For half of the beetle larvae, the leaf that they were observed on was experimentally clipped with dissecting scissors at the start of the hour-long observation period in the field. Sagebrush leaves have three lobes and one of these lobes was clipped during the treatment. Two other nearby leaves (within 2 cm) also had one of their lobes clipped for plants assigned to this treatment. The other beetles served as controls and the leaf they were on plus two others nearby were touched, but not clipped, by the scissors. After one hour, we observed the location of each larva – whether it stayed on the original leaf or moved.

Second, we returned to each marked location after 24 hours and recorded whether we could locate each of the beetle larvae on the original branch. We selected plants that had low densities of beetles for this experiment. It is possible that some of the beetles that we located after 24 hours were not the original ones that we had marked the previous day. Because there were few beetles (2-10) on these bushes, this is unlikely and there is no reason to imagine that treatment should have affected the frequency of this outcome. We assume that beetle larvae rarely moved between bushes because we observed similar numbers of beetles on successive days (pers. obs).

Third, we tested whether beetle larvae were more likely to move if neighboring leaves were clipped. We marked the location of 100 larvae with lab tape. For half of the larvae, we clipped the tip of three leaves that were physically close to each larva (within 2 cm) but not the leaf that the larva was on. Some of the clipped leaves were not on the same stem or sharing vascular connections with the leaf that the larva was on. After 24 hours we recorded whether each larva had moved from its original location.

Fourth, we attempted to repeat the experiments by introducing the beetles to leaves receiving different treatments. We tested whether 60 larvae would be more likely to move after 24 hours if they were placed on experimentally clipped leaves compared to being placed on unclipped control leaves in the field.

For each of the movement experiments above, we used Fisher's exact test to compare whether larvae were more likely to move from treated leaves compared to untreated controls. Since we had the *a priori* expectation that beetles would be more likely to move from damaged leaves or leaves receiving cues from damaged leaves, these tests were one-tailed.

Dispersion of damage

We evaluated the pattern of dispersion of beetle damage on bushes early in the feeding season (July 10) and later after larval feeding had finished (August 24). We mapped all of the branches (mean = 11.7 branches) on 10 bushes and recorded the number of leaves with damage caused by *T. pilosa* and the total number of leaves on each branch both early (July) and late (August). For each branch we calculated the mean number of leaves with beetle damage; a branch was the sampling unit. Since branches had different total numbers of leaves, we standardized these measures by calculating the proportion of damaged leaves per branch. We assessed whether the mean proportion of damaged leaves increased later in the season using a Wilcoxon signed-ranks test with repeated measures of damage (Sokal and Rohlf 1969). Since we had a clear *a priori* expectation, we used a one-tailed test. We chose this nonparametric approach because our damage data could not meet assumptions required for parametric analyses even with transformation (see Supporting Information).

We calculated the among-branch variance in proportional damage for each bush to assess if damage variability decreased between July and August. We tested the hypothesis that the variation among branches decreased as the season progressed using a Wilcoxon signed-ranks test with repeated measures of damage (Sokal and Rohlf 1969). Since we had a clear *a priori* expectation, we used a one-tailed test. We chose a nonparametric approach because our variance data could not meet assumptions required for parametric analyses, even with transformation (see Supporting Information).

Estimating the proportion of leaves that received chewing damage by *T. pilosa* was relatively quick and most importantly, did not require destructive sampling. However, many ecologists are accustomed to estimating damage by chewing herbivores as the percentage of leaf area that is removed. In order to compare these two methods, we removed one branch from 20 sagebrush plants that had varying levels of beetle damage. These branches were collected from another population of *A. tridentata vaseyana* near Tahoe meadows, Mt. Rose, Washoe County, Nevada (N 39.298 W -118.923). For each branch we estimated the number of leaves that had beetle damage standardized for 100 leaves (percent of leaves with damage) and also recorded the percent of leaf area removed by beetles for all of the leaves on each branch. Percent leaf area removed was estimated by photographing each leaf and using the LeafByte application

(Getman-Pickering, Campbell, Aflitto, Ugine, & Davis 2019). We compared levels of damage estimated as % leaves with damage, the measure used here, and as % leaf area removed using JMP 14.2 (Fit y by x).

We found that the percentage of leaves that had damage by beetles was a good predictor of the leaf area removed (Fig. 1, R^2 = 0.51, n = 20, P < 0.001). Since beetles eat only a small fraction of each leaf, the percentage of leaf area removed was approximately an order of magnitude less than the percentage of leaves that were damaged (the slope of the relationship in Fig. 1 was 0.087 $\pm$ 0.020 s.e.).

3 RESULTS

3.1 Movement

Beetles were more likely to move from those leaves that had been clipped compared to unclipped control leaves within one hour following clipping (Fig. 2, Fisher's exact test P = 0.002). After 24 hours, those beetles that had been on clipped leaves were more likely to have departed the branch compared to beetles on unclipped controls (Fig. 3, Fisher's exact test P = 0.02). Beetles that moved under these circumstances were most often not in the vicinity and had traveled some unknown distance. Since it was not feasible to mark the

beetles themselves without affecting their behavior, we were unable to determine how far they had moved.

The results were similar when nearby leaves were clipped but the leaf that the beetles were first on was not disturbed in either treatment. In this case, beetles were more likely to depart leaves whose neighbors had been experimentally clipped compared to those with unclipped neighboring leaves after one hour (Fig. 4, Fisher's exact test $P = 0.02$).

There was no difference in the likelihood that beetles placed on damaged leaves would move compared to beetles placed on undamaged leaves. For both of these treatments, 21 of 30 beetles moved off the leaf they had been placed on within the first hour (Fisher's exact test $P = 1.00$). Placing the beetles on experimental leaves appeared to agitate them and they moved almost immediately in most cases.

3.2 Dispersion of damage

The ten bushes that we selected to examine patterns of dispersion of damage ranged from having 4 to 65 percent of their leaves with damage during the early sampling event in July (Fig. 5A, mean 25 % of leaves had chewing damage). As the season progressed, more leaves received damage (the mean proportion of damaged leaves increased from 25% to 34%, Wilcoxon signed-ranks test, $P = 0.01$). Over this time period, the variance in the proportion of

leaves with damage decreased by 52% (Fig. 5B, Wilcoxon signed-ranks test, P = 0.019). Variance in the proportion of leaves decreased for 8 of 10 bushes even as the mean level of damage increased (Fig. 5C). The pattern of damage became less aggregated (more even) across the branches on individual plants.

4 DISCUSSION

We have learned a lot about the mechanisms of induced resistance and about their effects on the survival and performance of herbivores. However, we still know relatively little about how they affect the population dynamics of herbivores, particularly their spatial dynamics (Karban 2011, Rubin, Ellner, Kessler, & Morrell 2015). This is somewhat surprising since early reports of induced resistance against herbivory were motivated by observations of striking spatial patterns of damage (e.g., Carroll and Hoffman 1980, Edwards and Wratten 1983). Edwards and Wratten argued that herbivores would move away from damaged tissue and that this induced movement would create an even distribution of plant damage. For these early model systems, it is still not known whether either the plants or herbivores use volatile information to induce plant resistance or for informed herbivore movement.

Two theoretical models have considered the spatial distributions of damage that are predicted by induced plant responses. Underwood, Anderson, & Inouye (2005) modeled herbivore movement caused by

induction and found that herbivores tended to move away from damage and to aggregate at tissues of higher quality. Either aggregated or even distributions could result depending upon the time lags between initial damage, plant responses, and subsequent movement. A more recent model that included both informed herbivore movement and communication between plant tissues that affected induction found that time lags and the magnitude of informed herbivore movement and plant communication all influenced the distribution of damage (Rubin, Ellner, Kessler, & Morrell 2015). These models both predicted that aggregated, random, or even distributions can be expected. Informed herbivore movement led to aggregated damage but the combination of informed movement plus plant communication spread damage more evenly (Rubin, Ellner, Kessler, & Morrell 2015).

The current study is the first empirical test of predictions of Rubin et al.'s model in a system in which both herbivores and plants are known to use volatile information emitted by nearby plant tissues. *T. pilosa* larvae in the field were found to move away from leaves that were experimentally damaged (Figs. 2, 3) or were exposed to volatiles from experimentally damaged leaves (Fig. 4). They were more likely to choose to feed on leaves that were neither damaged nor exposed to volatiles from damaged neighbors in lab trials (Grof-Tisza et al. 2020). Sagebrush also perceives cues emitted by damage and becomes more

resistant to herbivores when it is exposed to volatiles from experimentally damaged tissue of the same or neighboring individuals (Karban, Shiojiri, Huntzinger, & McCall 2006).

As the season progressed, beetle larvae damaged a greater percentage of leaves (Fig 5A). We found that the non-destructive estimates of the proportion of leaves that were damaged by herbivores and destructive measures of leaf area removed were reasonably well correlated (Fig. 1). Not only did the mean level of damage increase over the season (Fig. 5A), but the variance in damage among branches on individual bushes decreased (Fig. 5B, C). The distribution of damage became more even as the season progressed and damage accumulated. This result was robust to our analytical methods; analyzing mean residuals for branches during early and late samples gave similar results as those we presented (see Supporting Information).

Many induced plant responses have been found to be localized, strongest for the semi-autonomous tissues near to the site of damage (Tuomi, Fagerstrom, & Niemela 1991, de Kroon, Huber, Stuefer & van Groenendael 2005, Zanne, Sweeney, Sharma & Orians 2006). In keeping with this generalization, induced responses of sagebrush to herbivory remain localized and information does not transfer readily among branches through the plant's vascular system (Cook and Stoddart 1960, Karban, Shiojiri, Huntzinger, & McCall 2006). Localized

plant responses increase the spatial variation among leaves and branches, i.e., increase within-plant patchiness in traits that affect herbivores. Many plants have recently been found to perceive and respond to volatile cues emitted by damage to neighboring plant tissues (Karban 2015). The effectiveness of volatile plant-plant communication dissipates over relatively short distances (Heil and Adame-Alvarez 2010, Karban 2015). Plant responses to localized volatile cues also tend to increase the patchiness of defensive and nutritive traits that affect herbivores.

Sharing information among plant tissues can have the opposite influence of evening out the variation in plant quality. For plants that perceive volatile cues, any particular plant tissue does not need to be damaged itself prior to responding to elevated risk. In this way, volatile communication has the potential to reduce variation in plant quality among tissues within an individual. Rubin et al. (2015) noted that those empirical studies that found that induced resistance made the distribution of damage more even (Edwards and Wratten 1983, Bergelson, Fowler, & Hartley 1986, Silkstone 1987) all described systems in which the number of leaves greatly outnumbered the number of herbivores. In these cases, the herbivores could move away from previously damaged leaves and seek out undamaged ones. This was also the case for *T. pilosa* and sagebrush in this study with the possible exception of two of the ten bushes that experienced

approximately 90% of all leaves with beetle damage by the end of the season. For these bushes, beetle larvae fed on most leaves within an individual plant canopy but they consumed relatively little leaf area on any given leaf (Fig. 1).

In conclusion, informed movement by *T. pilosa* larvae away from damaged sagebrush leaves over the course of their development had the effect of evening the distribution of damage among branches within individual bushes. The distribution of damage is not well studied but existing evidence suggests that it can be at least as important as the total amount of damage. Herbivores that dispersed their damage had less adverse effects on plant fitness compared to those with the same amount of more aggregated damage (Marquis 1992, Mauricio, Bowers, & Bazzaz 1993, Meyer 1998). Since sagebrush is a long-lived perennial, it was not feasible to assess the effects of different spatial patterns of damage on plant fitness in this system. Patterns of dispersion of damage can also affect key population properties such as dynamics and stability (Hassell and May 1973, Ives 1991, Cronin 2003); these patterns deserve more consideration in plant-herbivore studies involving systems that are more amenable to addressing plant performance. Distributions of damage that are even rather than aggregated are counter-intuitive; this system provides an example of induced plant responses to volatile cues coupled with

informed herbivore movement that shift the distribution of damage towards increased evenness.

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Authors' Contributions

RK designed the study and collected the data. RK and LHY analyzed the data and wrote the paper.

Data are available in Dryad https://doi.org/10.25338/B8162M

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536 206.

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538 Figure Captions

539 Fig 1. The relationship between the percentage of leaves damaged by
540 beetles and the percent area removed for 20 branches. (R^2 =
541 0.51, n = 20, $P < 0.001$).

542 Fig 2. The number of beetle larvae that moved away from leaves that
543 had been experimentally damaged (clip) versus unclipped
544 controls after one hour.

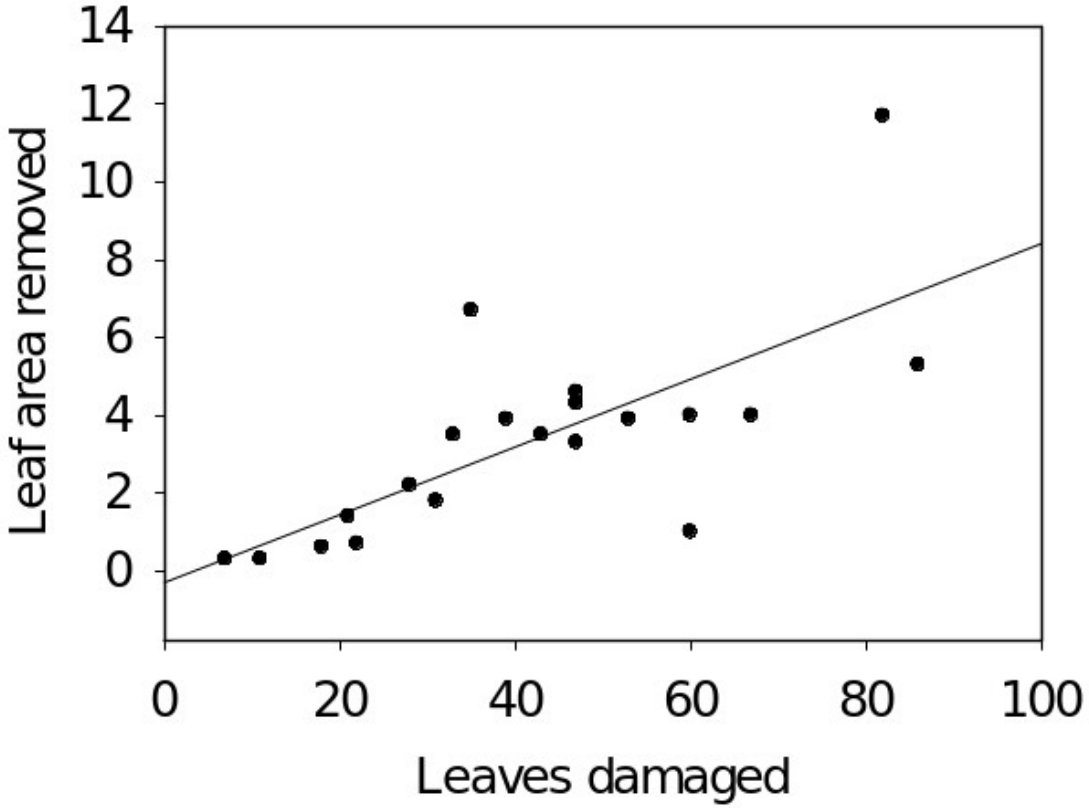
545 Fig 3. The number of beetle larvae that we were able to locate (stayed)
546 on branches that had been experimentally damaged (clip) versus
547 unclipped controls after 24 hours.

548 Fig 4. The number of beetle larvae that moved away from leaves that
549 had been exposed to volatiles from experimentally clipped
550 neighboring leaves versus unclipped controls after one hour.

551 Fig 5. The proportion of leaves on branches that have been damaged
552 by beetle feeding on ten sagebrush bushes soon after beetle
553 larvae began feeding (July - early season) and after beetle larvae
554 had completed feeding (August - late season). A. Mean
555 proportion of damaged leaves $\pm$ 1 s.e. B. Variance in the
556 proportion of damaged leaves $\pm$ 1 s.e. C. Change in the variance
557 in the proportion of damaged leaves for each of the ten bushes

over the season. The darker line indicates two bushes with similar values.

562 Fig. 1
563



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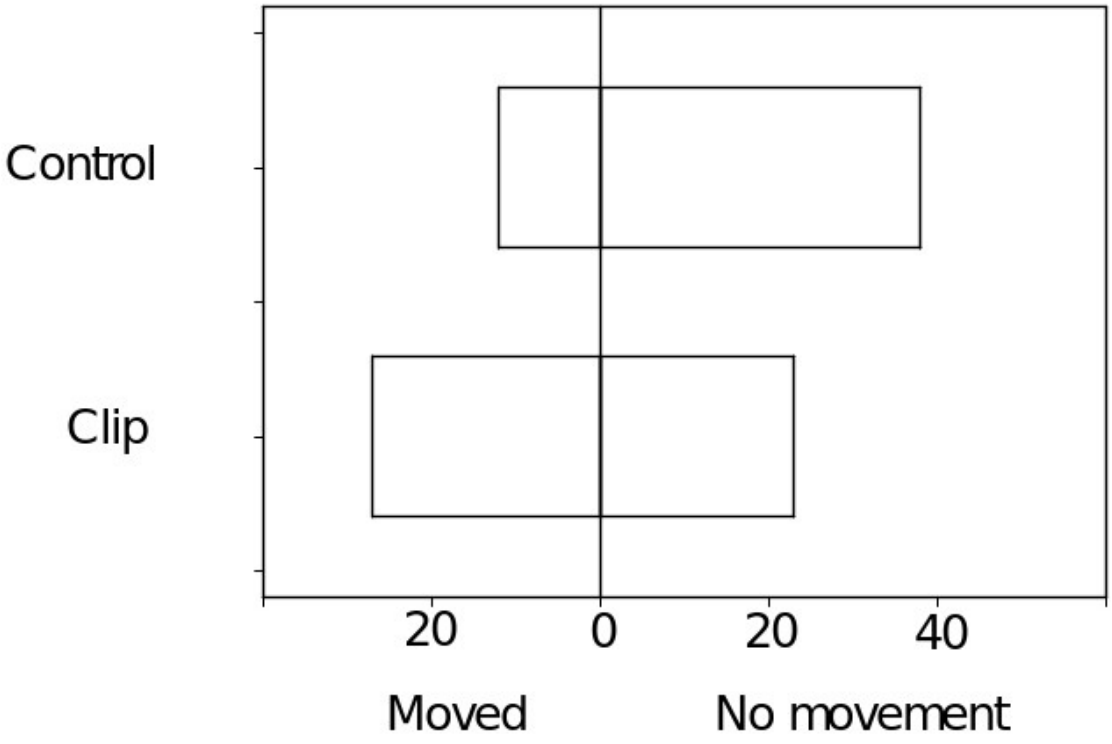
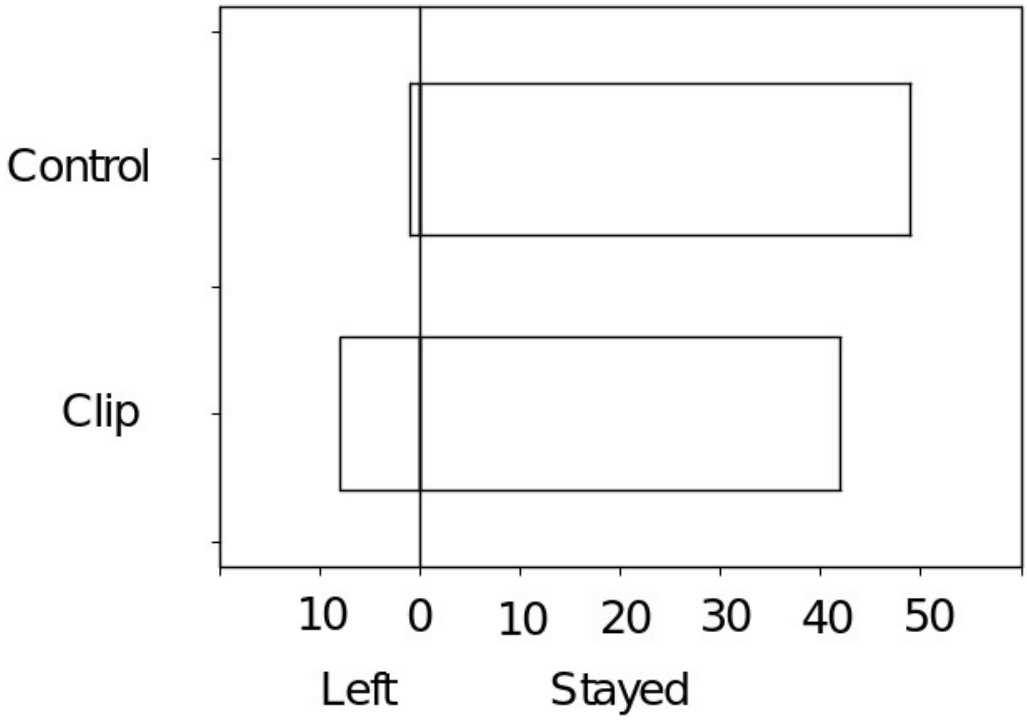
565

566 Fig 2



567

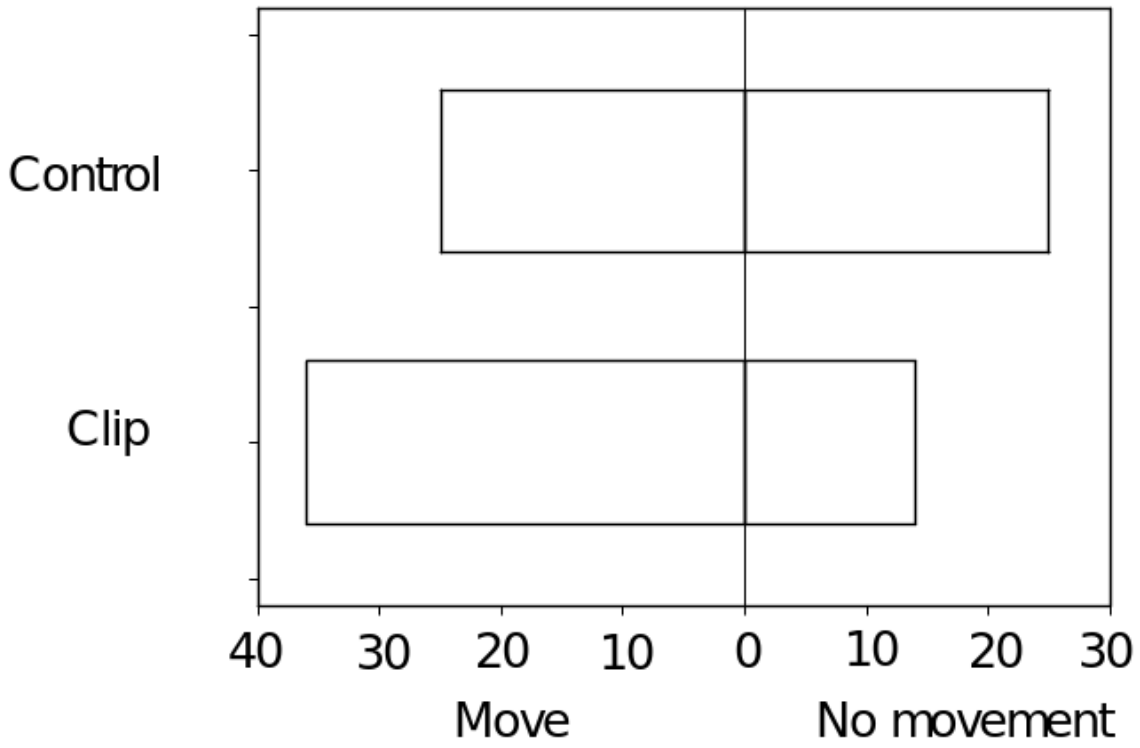
568



569

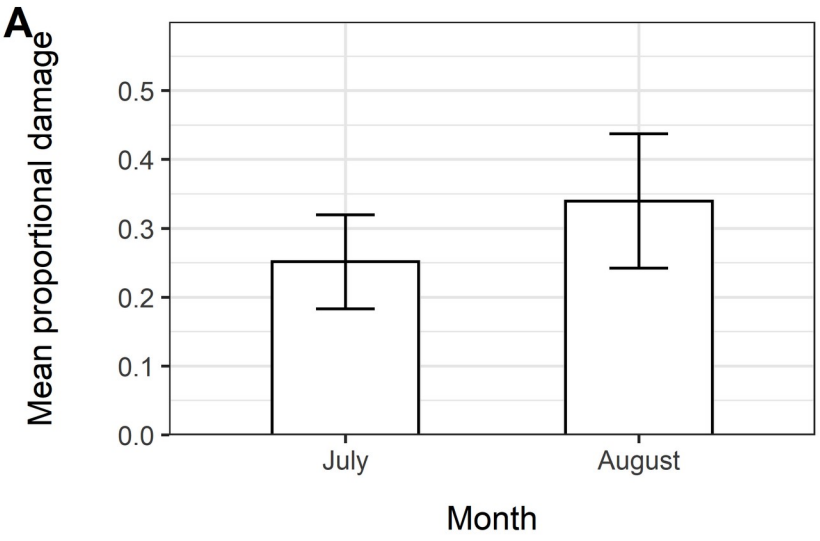
570 Fig 3
571

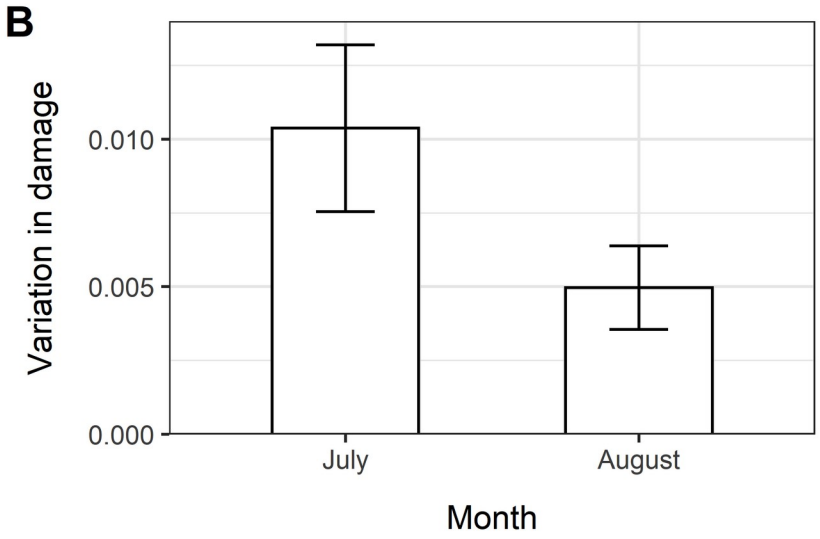
572 Fig 4

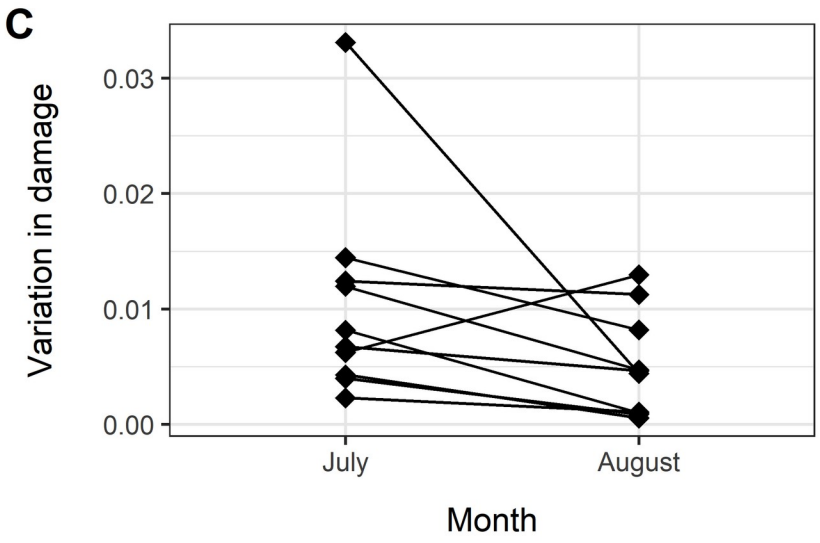


573

574 Fig 5


A
Mean proportional damage
0.5
0.4
0.3
0.2
0.1
0.0
July
August
Month


B
Variation in damage
0.010
0.005
0.000
July
August
Month


C
Variation in damage
0.03
0.02
0.01
0.00
July
August
Month

575

Supporting Information

Dispersion of damage

In our paper, we reported that the variation in the proportion of leaves on branches that were damaged by beetles was greater early compared to late in the season (Fig 5B, C). We obtained similar results when we considered the mean absolute residuals (i.e., mean residual deviance) from a linear model with proportional damage as the dependent variable, month as a fixed factor, and bush as a random factor to account for the repeated measures design. While variance is based on the sum of squared deviations, this analysis of residuals uses absolute values and is less sensitive to large deviations. Both analyses yielded qualitatively similar results. Mean absolute residuals decreased by 11.7% between July and August (one-tailed Wilcoxon ranked sum test, $P = 0.04$). This test is analogous to a non-parametric, repeated measures Levene test for equality of variances.

A non-parametric approach was required because the proportional damage data in this study did not meet the assumption of binomial, Poisson or other parametric analyses. While logit transformations are often recommended to allow for the parametric analysis of proportional data (e.g., Warton, D. I., and F. K. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10), this dataset included zero values and this made it unreliably

598 sensitive to the size of the arbitrary non-zero constant required to

599 transform these data.